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TWO NEW SPECIES OF SHEEP-LIKE ANTELOPE FROM THE MIOCENE OF MONGOLIA[1]

BY GUY E. PILGRIM[2]

The antelope remains which form the subject of this paper were collected in Mongolia in 1930 on the Tung Gur tableland (Lat. 43° 35′; Long. 112° 40′) by Dr. W. Granger, who has kindly entrusted them to me for description. The deposit is isolated from other Tertiary beds of known age, so that its exact stratigraphical relations cannot be observed. The fauna differs from that of the North China Red Beds with *Hipparion* and from the *Hipparion* fauna described by Schlosser from Inner Mongolia, both referred to the Pontian, and is considered to indicate that it belongs to a period previous to that, which may be the equivalent of the Sarmatian or even earlier.

The Oiocerine antelopes form the largest part of the fauna, at any rate after the Proboscidea, which include the very abundant *Platybelodon grangeri* and a single ramus of *Serridentinus gobiensis*, which have been described by Osborn and Granger (Amer. Mus. Novitates, Nos. 470, 1931, and 537, 1932). A Giraffoid of the *Palaeotragus* group is fairly common and Cervidae rather less so. There is a *Listriodon*, apparently closely allied to *L. pentapotamiae* common in the Chinji stage of India. Rhinocerotidae also occur. Equidae are extremely rare, but the absence of *Hipparion* seems to be significant, especially since a palate and lower jaws of the older genus *Anchitherium* have been recovered from these beds. Chalicotheres were present and show rather close relationship with *Macrotherium*. The Carnivora are represented by a fine skull of *Hemicyon*, by a *Hyaena* of the type of *Crocuta carnifex*, by an *Ictitherium* and by a felid closely allied to or identical with *Metailurus*. Rodents have also been found.

Both the Oiocerine species seem, by their short, upright and only slightly twisted horns, to be more primitive than the Pontian forms belonging to this group. It is true that one of them, **Oioceros (?) grangeri**, attains a larger size than any form hitherto ascribed to *Oioceros*, and therefore is probably a terminal species. On the other hand, **Oioceros (?)**

[1]Publications of the Asiatic Expeditions of The American Museum of Natural History. Contribution No. 124.

[2]Formerly of the Geological Survey of India.

noverca is a small species, which might have been ancestral to one of the Pontian oiocerines.

Oioceros Gaillard 1902

Oioceros GAILLARD, 1902. Bull. Soc. Anthropol. Lyon, XX, p. 93, fig. 8.

GENOTYPE.—*Antilope rothii* Wagner, 1857. Abh. Bayer. Akad. Wiss., VIII, p. 154, Pl. VI, fig. 20.

REMARKS

The genus *Oioceros* was founded by Gaillard (1902, p. 93) for the species *Antilope rothii* Wagner (1857, p. 154) from Pikermi, provisionally referred by Gaudry (1865, p. 297) to the living genus *Antidorcas*. Until now four other species have been included in *Oioceros*. These are: *Antidorcas* (?) *atropatenes* Rodler and Weithofer (1890, p. 767) from Maragha; *Oioceros* (?) *proaries* Schlosser (1904, p. 73) from Samos; *Oioceros boulei* De Mecquenem (1925, p. 13) from Maragha; *Oioceros wegneri* Andree (1926, p. 170) from Samos.

De Mecquenem (1925, p. 12, Pl. VII, fig. 7) very briefly described and figured a skull from Maragha, which he attributed to *Oioceros rothii*. Professor Boule has kindly afforded me an opportunity of studying the specimen in Paris, but I do not find myself in agreement with De Mecquenem on the specific identification. The poor state of preservation of the horn-cores, which are not only fractured near the base but are also much battered, does not, in my opinion, permit even the reference to *Oioceros* to be made with certainty. At the same time the expansion of the orbital roof, the character of the upper molars, which are very similar to those of *Oioceros boulei* and **Oioceros** (?) **grangeri**, and the structure of the basicranium, which recalls that of *O.* (?) *grangeri*, render the generic reference probable. The faint ribbing still visible on the horn-cores shows no character which would tend to contradict this opinion. The much greater backward tilt and the much greater divergence of the horn-cores seem to render the reference to *Oioceros rothii* out of the question. In regard to the former character, it resembles *O. boulei;* in the latter it is approached only by *Oioceros wegneri* and *Ovis kuhlmanni* Andree; in both these last, however, the horn-cores are much larger. There is some resemblance between the Maragha skull and the hornless skull from Samos described and figured by Schlosser under the name of *Oioceros* (?) *proaries*, as will be seen from the table of measurements on pages 24–26. The outline of the skulls, the degree of bending down of the face on the cranial axis, and the shortness of the occiput are alike in both. Considering, however, the greater size of the teeth in *Oioceros* (?) *proaries*, many of the relative dimensions of the two skulls are less

close than would appear at first sight, especially the height of the face which is greater in *O.* (?) *proaries* and the size of the occipital which is relatively smaller in *O.* (?) *proaries*. For this reason I think that the Maragha and Samos skulls should be specifically distinguished, and I propose for the former the name of **Oioceros** (?) **mecquenemi.**

Besides this, two other species are now added: **Oioceros** (?) **grangeri,** n.sp., and **Oioceros** (?) **noverca,** n. sp., from Mongolia, not because I am in any doubt that modern usage in zoological classification would justify their generic separation, but because many of the other species listed above are probably equally entitled to rank as separate genera, though their material is insufficient to enable satisfactory diagnoses to be given. In fact the only characters of generic value which they possess in common, so far as material for comparison exists, are the counter-clockwise torsion of the horns (right); the expanded orbital roof; the square and precociously hypsodont upper molars. The diagnosis of *Oioceros* given by Pilgrim and Hopwood (1928, p. 24) was expressly framed so as to be comprehensive and serves to bring out the divergencies of the species amongst themselves. At the same time the eight species form a well-defined group, probably of subfamily rank, confined to the Sarmato-Pontian and showing affinities both to the Ovicaprinae and to the Rupicaprinae. In these circumstances I do not think any useful purpose would be served at present if I were to attempt to divide them into genera or even to frame a generic diagnosis for *O.* (?) *grangeri* and *O.* (?) *noverca*, which are the two most completely known of them all.

The same argument would probably favor the provisional inclusion in the genus *Oioceros* of the species from Samos described by Andree (1926, p. 172) under the name of *Ovis kuhlmanni*, especially as from Andree's description we are led to suppose that the hornless skull from Samos which Schlosser called *Oioceros* (?) *proaries* is the female of an allied species. In any case I do not think that the square molars and the more brachyodont character of the teeth are in accord with the reference to *Ovis*. *"Ovis" kuhlmanni* apparently represents an advanced form of the group we are considering, in virtue of the great bending down of the face on the occiput, its long horns and shortened parietals, and so naturally bears a greater resemblance to the living sheep than most other members of the *Oioceros* group. On the contrary, *Oioceros* (?) *grangeri* and *O.* (?) *noverca* are probably near the other end of the scale, since their short, simple, upright, slightly twisted horns indicate that they are in a more primitive stage than other species of *Oioceros*. No doubt the Samos no less than the Mongolian species represents a distinct

generic type, but to include it in the living genus *Ovis* is, in my opinion, hardly a procedure calculated to assist palaeontological research.

Oioceros (?) grangeri, new species

HOLOTYPE.—Amer. Mus. No. 26508, skull.

PARATYPES.—Amer. Mus. No. 26509, skull; Amer. Mus. No. 26516, left mandibular ramus.

HORIZON AND LOCALITY.—Wolf Camp Quarry. Fifty miles southeast of Iren Dabasu, Inner Mongolia. From the Tung Gur formation, Upper Miocene.

DIAGNOSIS.—An *Oioceros* of larger size than any of the other known species; with face bent down on occiput at an angle of about 30°; breadth of skull at orbits very great; face long; horn-cores standing far apart on the frontals, directly above the orbits, rather upright, forming with the plane of the face an angle of as much as 55° and approximately at right angles to the plane of the occiput; approaching one another up to about one-third their length from the base and then diverging up to the tip, much shorter than in any other species except *O.*(?) *noverca*, very slightly twisted, not more than one-quarter of a revolution, stout at the base, cross-section almost circular, without a noticeable keel but with numerous coarse anastomosing ribs which follow the torsion of the horns from base to tip, placed on very long pedicles; with a deep lachrymal fossa; fronto-parietal suture far forward, about 17 mm. behind the horn-cores, with a strong swelling round it; occipital surface very concave, in a vertical as well as in a horizontal direction; strong and overhanging lambdoid crest; teeth rather hypsodont; molars relatively large; premolar series short relative to molar series.

DESCRIPTION

The holotype skull is in a fairly perfect state of preservation, the only essential parts missing being the nasals and premaxillae. These are supplied by another skull from the same locality, Amer. Mus. No. 26509, in which the horn-cores, teeth and basicranium are less perfectly preserved. In the holotype the hinder part of the right maxilla is defective and M^2 and M^3 are missing or broken, but the left maxilla and the entire cheek dentition on that side are perfectly preserved. The face is very slightly crushed in the lateral plane. The skull is that of a fully grown animal, since the last molar is somewhat worn. It seems to have been an unusually large individual of the species, since out of some twenty sets of teeth which cannot be separated specifically, those of the holotype are the largest.

The face is bent down on the cranial axis at an angle of about 30°. In relation to the length of the occiput, the face is long, as much so as in the living genus *Ovis* and much more so than in *Capricornis, Nemorhaedus* or *Capra*. The skull is extremely broad at the frontals, its width between the orbits considerably exceeding the distance between the hinder margin of the orbit and the occipital condyles.

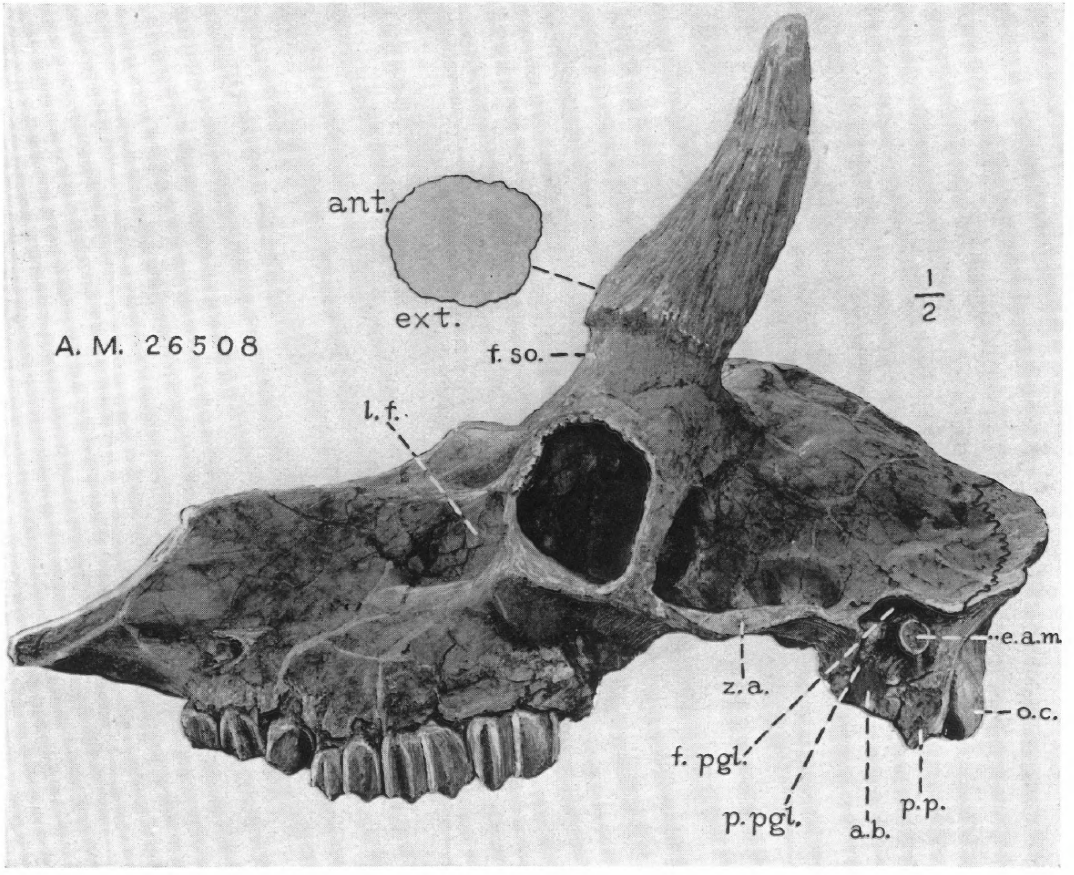

Fig. 1. *Oioceros* (?) *grangeri*, new species, A. M. No. 26508, type. Lateral view of skull with cross section of horn-core at base. One-half natural size. a.b., auditory bulla; e.a.m., external auditory meatus; f. pgl., postglenoid foramen; f.so., supraorbital foramen; l.f., lachrymal fossa; o.c., occipital condyle; p. pgl., postglenoid process; p.p., paroccipital process; z.a., zygomatic arch.

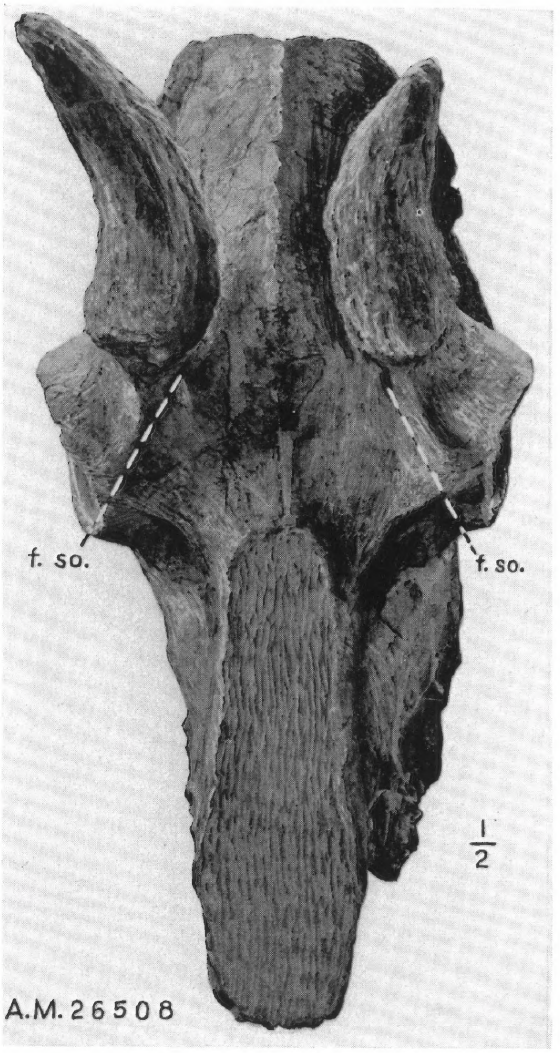

Fig. 2. *Oioceros* (?) *grangeri*, new species, A. M. No. 26508, type. Superior view of the skull. One-half natural size. f.so., supraorbital foramen.

The horn-cores are situated immediately above the orbits, and if the occiput be placed in a horizontal position, the hinder edge of the horn-core almost coincides with that of the orbit. The horn-cores are placed on exceptionally long pedicles, which lie very far apart from one another on the frontals; they are rather upright, being approximately at right angles to the plane of the occiput and forming an angle of about 55°

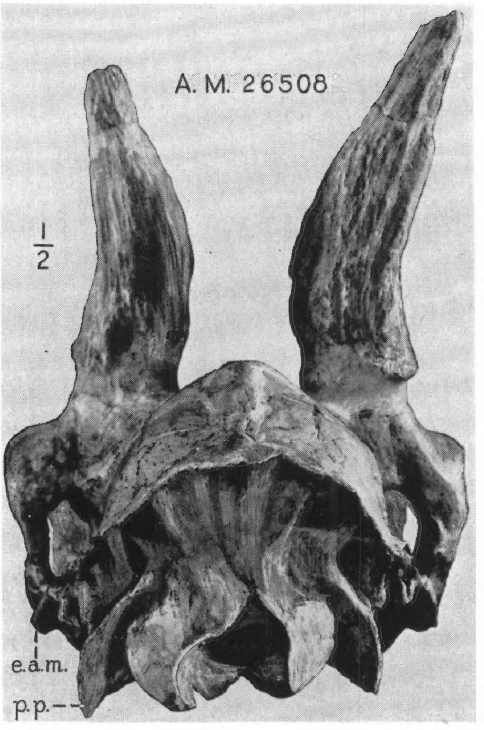

Fig. 3. *Oioceros* (?) *grangeri*, new species, A. M. No. 26508, type. Posterior view of skull. One-half natural size. e.a.m., external auditory meatus; p.p., paroccipital process.

with the plane of the face; they are much shorter than is usual in the genus *Oioceros*, but are stoutly built, with a cross-section broadly oval at the base, the long axis being rather oblique to the cranial axis; they are twisted spirally in a counter-clockwise direction (i.e., for the right horn), but to a very slight extent, the torsion from base to tip not amounting to as much as a quarter of a revolution. There is no noticeable keel, but the surface of the horn-core is covered with numer-

ous anastomosing ribs, which follow the direction of torsion of the horn. The torsion causes the horn-cores to approach one another for about one third of their length and then to recede from one another up to the tip.

The highest point of the skull is at the fronto-parietal suture, which is convex towards the rear and is situated about 17 mm. behind the horn-cores. Round this point is a lozenge-shaped inflated area, which is continued both to the front and the rear as a swelling on the parietal suture and on the frontal suture between the horn-cores. In front of the horns the frontals are depressed and the suture itself is flat; the surface rises again to the fronto-nasal suture.

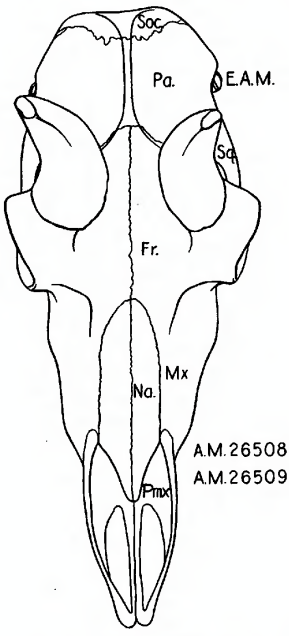

Fig. 4. *Oioceros* (?) *grangeri*, new species. Composite diagram of skull from above. Based on A. M. No. 26508, type, and A. M. No. 26509, paratype. One-fourth natural size. E.A.M., external auditory meatus; Fr., frontal; Mx., maxilla; Na., nasal; Pa., parietal; Pmx, premaxilla; Soc., supraoccipital; Sq., squamosal.

The orbits are of moderate size, almost circular, and their upper margins project considerably beyond the base of the horn-cores. The supra-orbital foramina open into small, narrow, vertical fossae, situated in the pedicles of the horn-cores, and are overhung by the latter. The lachrymal fossae are deep, though less so than in many recent species of *Ovis*. An ethmoidal fissure, if present at all, is of trifling extent.

The nasals are long and narrow; they indent the frontals at an acute angle and reach back almost to the level of the anterior edge of the orbits; their anterior ends are missing in the skull No. 26509, but one may estimate that their tips extended about 20 mm. in front of P^2. They articulate with the lachrymals and maxillae until they reach the hinder end of the premaxillae, with which they also articulate, though to a less extent than in *Capra*. In *Ovis* the nasals do not articulate either with the maxillae or the premaxillae. The premaxillae are exceptionally long, even more so than in *Ovis*. They run up between the nasals and the maxillae, with both of which they articulate as in *Capra*, though in that genus the length of the articulation is greater. In *Ovis* the articulation of the premaxilla with the maxilla is longer than in *Oioceros* (?) *grangeri*, but the premaxillae do not articulate with the nasals, although almost in contact

with them. In any case the condition in *Capricornis, Nemorhaedus, Rupicapra, Budorcas* and *Ovibos* is entirely different from that in *Oioceros* (?) *grangeri,* since the premaxillae end far in front of the articulation of the nasals with the maxillae.

The brain-case is rather narrow behind the horn-cores, which project considerably beyond it, but widens somewhat to the rear. There are no temporal ridges. A prominent sagittal crest existed, though it is broken off in the holotype.

The supraoccipital occupies a broad area on the surface of the skull, but does not extend very far forward, the suture with the parietal being perfectly clear. The lambdoid crest is very prominent and considerably overhangs the occipital which is extremely hollowed both in a vertical and in a horizontal direction. The occipital has a broadly semi-oval shape; it is rather low, its breadth being much in excess of its height. The occipital crest is shown in the center of its hollow surface. The foramen magnum is not large and the condyles hardly project backward beyond the summit of the occipital crest. The paroccipital processes are rather extended in the anteroposterior direction but are not long. The mastoid process is weakly developed.

The basicranium presents several points of interest, especially since most of the forms hitherto referred to the genus *Oioceros* do not appear to have provided material sufficiently well preserved to admit of satisfactory study. At any rate I have seen no description of the basicranium of any species of *Oioceros.* The basioccipital is subtriangular in shape with a regularly rounded surface on which a median groove is indicated from the foramen magnum up to a point slightly in advance of the posterior tuberosities. The posterior tuberosities show a moderate lateral expansion but have not the great prominence which we find in the oxen. In front of them, narrowing proceeds regularly throughout the course of the basioccipital and basisphenoid, and there is a considerable interval between the basioccipital and the tympanic bulla. The anterior tuberosities are very small, and lie immediately opposite the postglenoid crest. The auditory bulla is small and in particular very short, hardly reaching farther forward than the postglenoid crest; it is but little inflated and projects but little below the level of the basioccipital; its summit forms a sharp-ridged crest in continuation of the antero-posterior diameter of the paroccipital process; internal to this crest the surface of the bulla slopes gently towards the inner side; on the outer side a slight invagination tends to encircle the attachment of the hyoid. The meatal tube projects strongly. Beneath it the very large stylomastoid

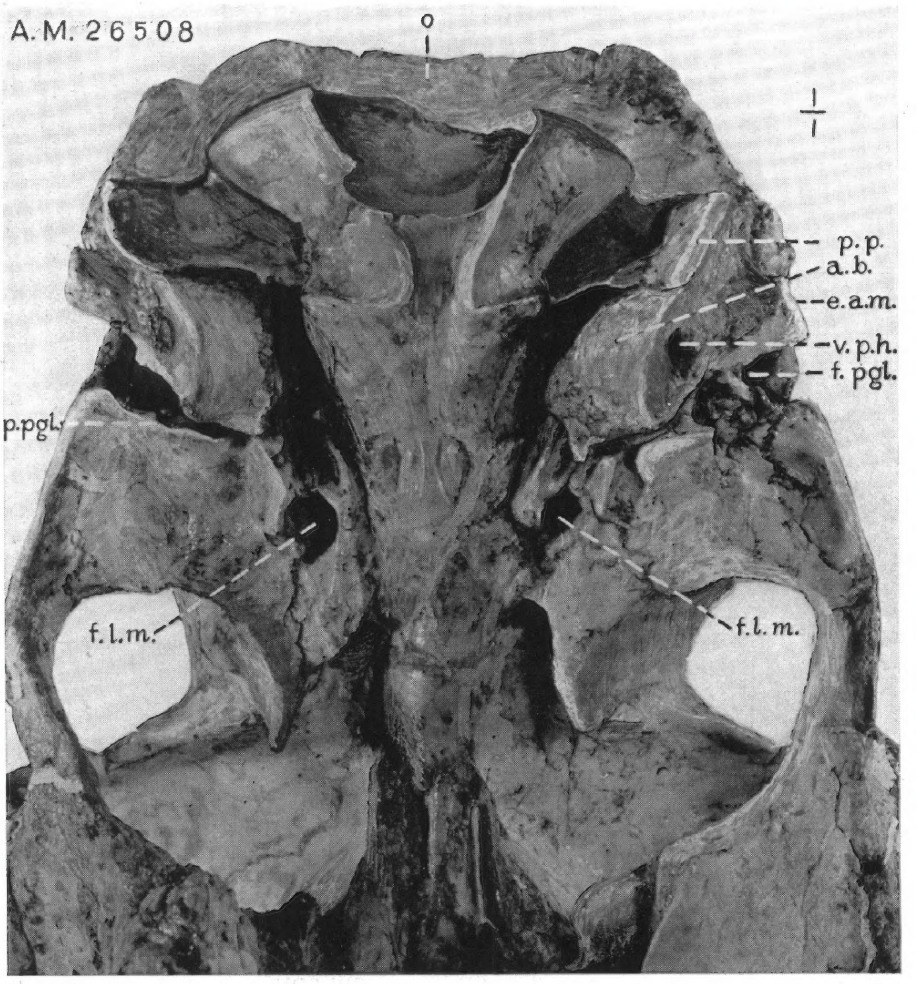

Fig. 5. *Oioceros* (?) *grangeri*, new species, A. M. No. 26508, type. Inferior view of posterior half of skull. Natural size. a.b., auditory bulla; e.a.m., external auditory meatus; f.l.m., foramen lacerum medium; f.pgl., postglenoid foramen; o., occiput; p.p., paroccipital process; p.pgl., postglenoid process; v.p.h., vagina processus hyoidei.

foramen is exposed, communicating by a small opening with the upper side of the squamosal. The bar of bone which separates the latter foramen from the outer margin is very slender. The foramen lacerum medium faces entirely downward and has bony ridges on either side of it.

Upper Dentition.—The molar series is rather long for the size of the skull both as compared with other species of *Oioceros* and also with living species of *Ovis*, *Capra*, *Nemorhaedus* and *Capricornis*. On the other hand, the premolar series is short as compared with other species of *Oioceros*, as well as with the living *Nemorhaedus* and *Capricornis*, but is longer than in *Ovis* and *Pseudois nahura*. The length of the molars but little exceeds the breadth. The crown height in the case of an unworn molar is approximately equal to the length. The median as well as the anterior and posterior folds on the outer side of the molars are very strong. There is a broad but little prominent median rib on the anterior lobe; this is practically absent on the posterior lobe. Median basal pillars are often quite absent on the inner side of the molars and in any case when present are very weak. The three upper premolars approximate in length very nearly to one another, P^4 being slightly the shortest. The transverse diameter decreases in the series from behind forward. Long spurs in most cases project into the central cavity of the upper premolars, producing islands after a moderate amount of wear. The enamel on all the teeth is smooth and unwrinkled.

Lower Dentition.—The same relation in size between the molars and the premolars holds in the lower as in the upper dentition. At the anterior end of the molars there is a well-marked fold both on the inner and on the outer side, but it is much stronger on the outer side. On the contrary at the posterior end of the molar there is only a weak fold on the inner side and none at all on the outer side. A fairly strong median basal pillar is present on the outer side of each one of the three molars. The talonid of M_3 is narrow and triangular. P_4 is primitively constituted, the inner cusp being separated by two clefts, which persist almost to the base of the crown, from the two anterior and the two posterior wings. In the external wall, about one-third the way from the front end, there is a deep furrow. P_3 is shorter but has the same structure. An additional low cusp is present at the base of the anterior of the two valleys. P_2 is still shorter; there is no inner cusp; the wings are short, the anterior one especially so. So far as can be seen, considering the much-worn condition of the incisors, their size seems to diminish from I_1 to I_3, but the difference is not greater than is usual in the living members of the Ovinae and Rupicaprinae and is quite incommensurate with what obtains in *Antidorcas*, in which I_1 is enormously enlarged.

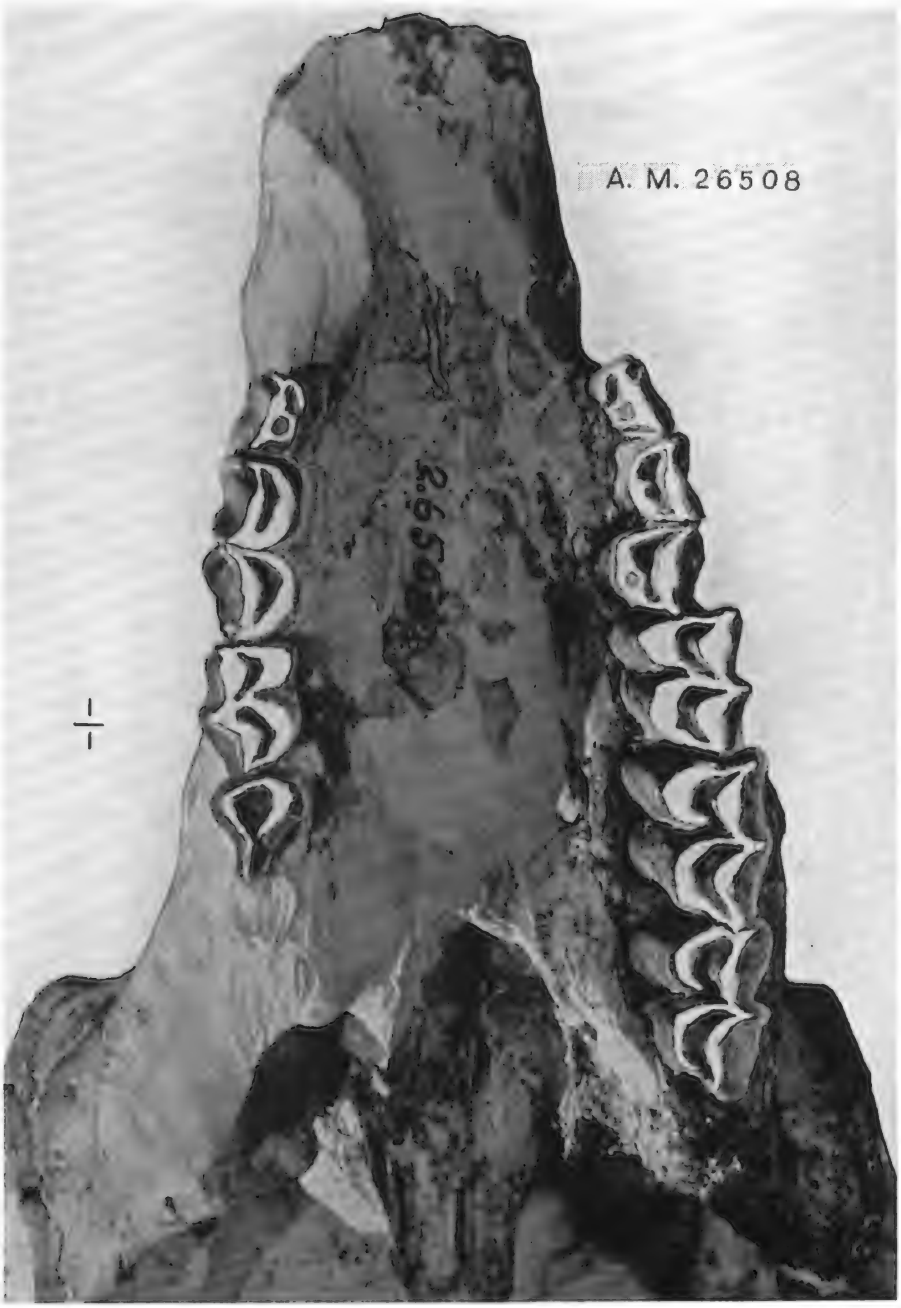

Fig. 6. *Oioceros* (?) *grangeri*, new species, A. M. No. 26508, type. Palatal view of anterior portion of skull. Natural size.

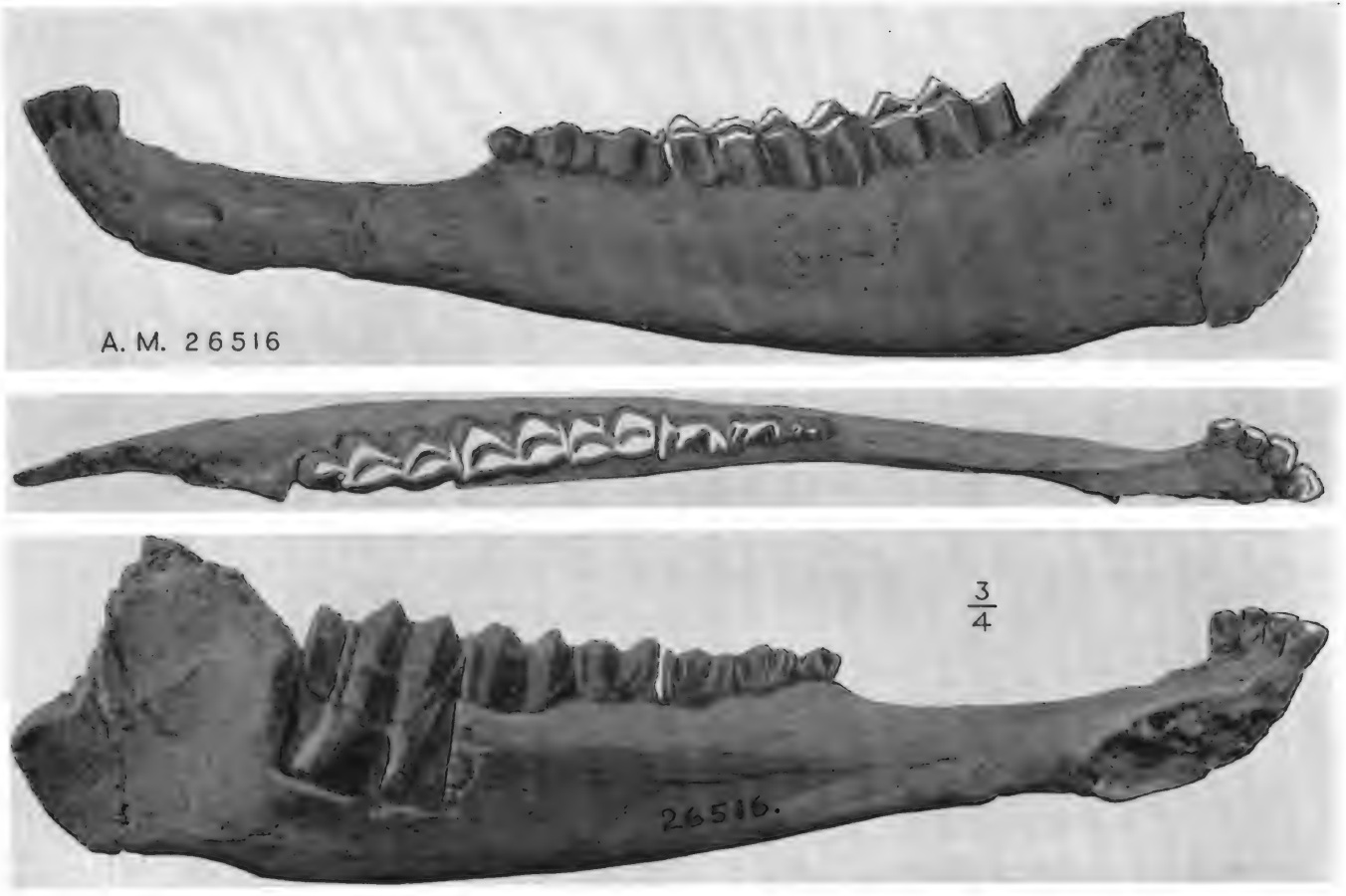

Fig. 7. *Oioceros* (?) *grangeri*, new species, A. M. No. 26516, paratype. Lower jaw: outer, superior, and inner views. Three-fourths natural size.

The diastema between P_2 and the incisors is somewhat longer than in *Ovis*, *Pseudois* and *Nemorhaedus*, from which we may draw the same conclusion as from the skull: that *Oioceros* (?) *grangeri* had a longer face and mandible than the living Ovinae and Rupicaprinae. On account

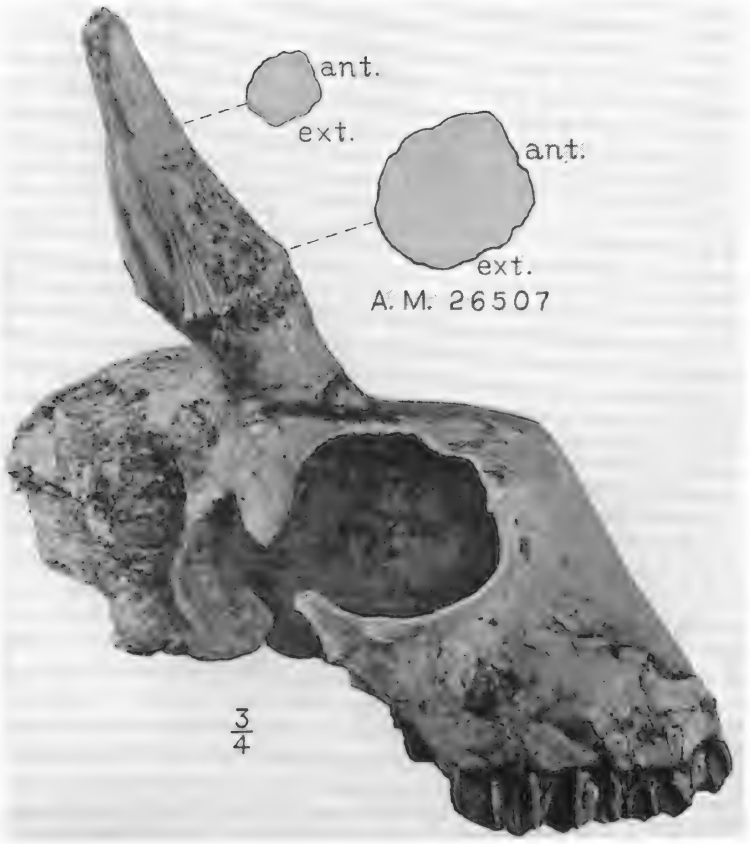

Fig. 8. *Oioceros* (?) *noverca*, new species, A. M. No. 26507, type. Side view of skull with cross sections of horn-core at base and near tip. Three-fourths natural size.

of the poor state of preservation of most of the other species of Oiocerinae, it is difficult to be sure whether the same condition obtained as in the Mongolian species, but it seems highly probable that it was so in *O.* (?) *proaries*, "*Ovis*" *kuhlmanni* and *O. wegneri*.

Fig. 9. *Oioceros* (?) *noverca*, new species, A. M. No. 26507, type. Anterior view of skull. Three-fourths natural size.

Oioceros (?) noverca, new species

HOLOTYPE.—Amer. Mus. No. 26507, skull.

PARATYPES.—Amer. Mus. 26223, frontlet; Amer. Mus. No. 26513, left maxilla; Amer. Mus. No. 26515, left mandibular ramus; Amer. Mus. No. 26501, back part of skull.

HORIZON AND LOCALITY.—Wolf Camp Quarry. Fifty miles southeast of Iren Dabasu, Inner Mongolia. From the Tung Gur formation, Upper Miocene.

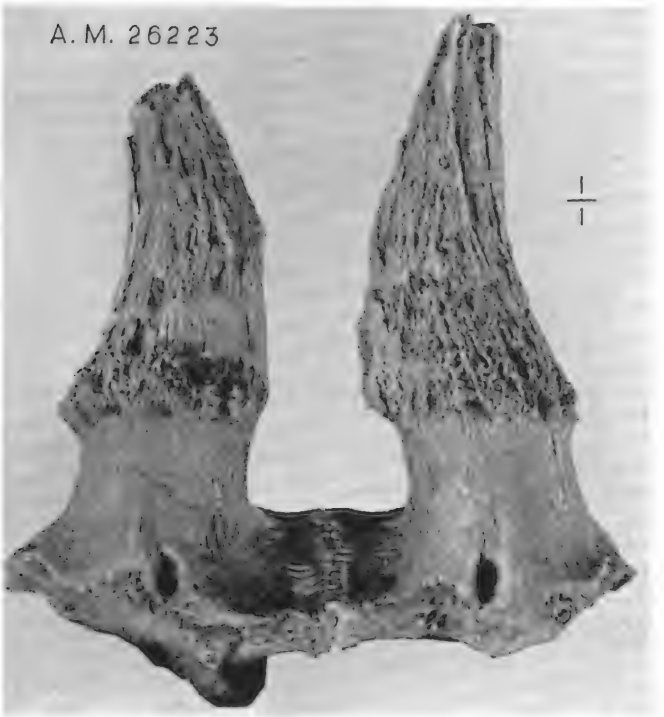

Fig. 10. *Oioceros* (?) *noverca*, new species, A. M. No. 26223, paratype. Anterior view of skull fragment supporting horn-cores. Natural size.

DIAGNOSIS.—An *Oioceros* of about three-quarters the size of *Oioceros* (?) *grangeri* with similar characters and differing only in the following particulars:—premolar series longer; area around the fronto-parietal suture less swollen; basioccipital tending slightly more to an oblong and less of a triangular shape; P_2 rather more complicated with an extra wing on the inner side.

DESCRIPTION

The holotype lacks most of the occiput and the premaxillary region but shows the frontlet as well as the orbits and maxillae, in which are the

much-worn teeth. The frontals above and anterior to the orbit seem to be somewhat distorted. The deficiency as to the hinder part of the skull is supplied by another specimen, Amer. Mus. No. 26501, which shows the basicranium. The upper dentition is better shown on an isolated left maxilla, Amer. Mus. No. 26513. Amer. Mus. No. 26223 is an isolated frontlet, which shows what seems to be the normal structure well, and

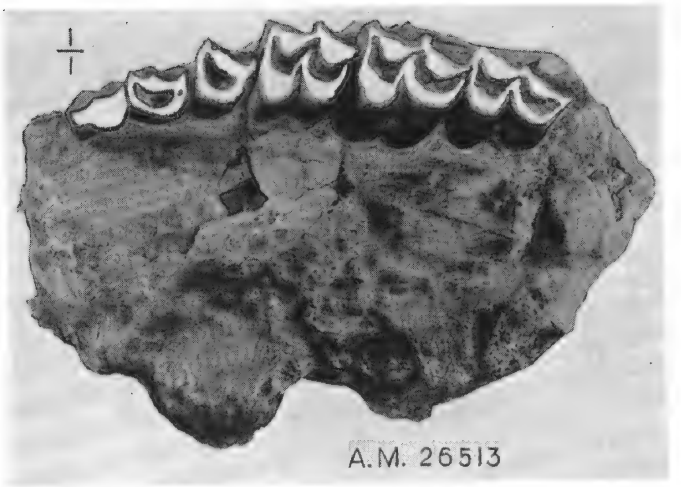

Fig. 11. *Oioceros* (?) *noverca*, new species, A. M. No. 26513, paratype. Palatal view of left maxilla with cheek teeth. Natural size.

the position of the supraorbital foramina. The left mandibular ramus, Amer. Mus. No. 26515, agrees in size with the skull. It belonged to a juvenile individual, and M_3 is but little worn. It lacks the angle and condyle and the incisor region, but shows the cheek-teeth well.

The agreement with *O.* (?) *grangeri* is very close except in size. The slight differences are sufficiently indicated in the diagnosis.

AFFINITIES OF THE MONGOLIAN SPECIES

The characters by which the two Mongolian species of *Oioceros* differ from those hitherto known seem chiefly to concern the structure and insertion of the horn-cores. They are much shorter, and although the character of the torsion is the same, namely counter-clockwise (i.e., for the right horn-core), it is much less in amount, being only about a quarter of a revolution as against about one revolution in *O. rothii*, *O. wegneri* and "*Ovis*" *kuhlmanni*, rather less than this in *O. boulei*, and about two

revolutions in *O. atropatenes*. The horn-cores of the two new species are almost circular in cross-section like those of *O. atropatenes*. In *O. boulei* and *O. wegneri*, they are quite circular, while in *O. rothii* they are more compressed laterally; in "*Ovis*" *kuhlmanni* extremely so. Those of *O.* (?) *mecquenemi* appear to resemble *O. rothii* in regard to their compression. The Mongolian horn-cores possess no trace of a definite keel nor of the external furrow which is so characteristic of *O. rothii*, and so resemble the horn-cores of *O. boulei* and possibly of *O.* (?) *mecquenemi* more nearly. All the other species have two or three well marked keels. In comparison

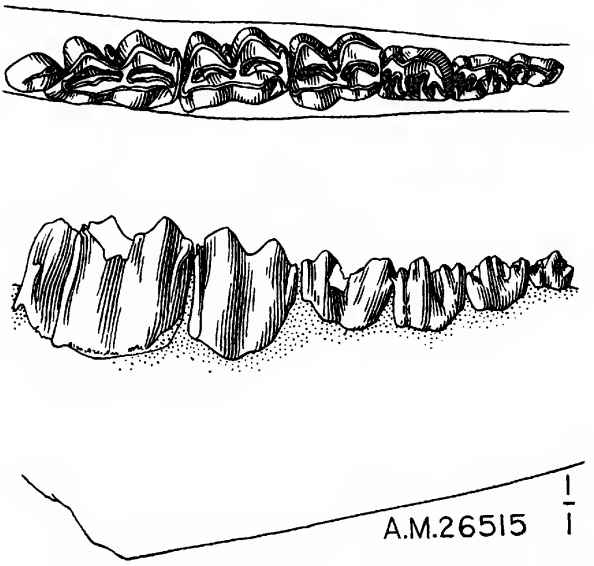

Fig. 12. *Oioceros* (?) *noverca*, new species, A. M. No. 26515, paratype. Left mandibular ramus showing crown and inner views of cheek teeth. Natural size.

with their length the Mongolian horn-cores are rather robust, though much less so than in *O. wegneri*. Relatively to the size of the skull, the diameter of the horn-core at the base is greater than in *O. boulei* and *O. atropatenes* but less than in *O. rothii* and *O.* (?) *mecquenemi* and much less than in "*Ovis* " *kuhlmanni*. The long pedicles of the horn-cores in the Mongolian species are very characteristic. No other species of *Oioceros* has them equally developed. The position of the supraorbital foramina at their base is not unlike a specimen of *O. rothii* from Maragha figured by De Mecquenem (1925, Pl. VII, fig. 4). The distance apart of the horn-cores at their base is relatively greater than in the other species and is to

be correlated with the greater width at the orbits. This distinction appears to be less marked in *O. atropatenes* and *O. boulei;* while on the contrary it is much more emphasized in *"Ovis" kuhlmanni;* and in *O. wegneri* the bases of the horn-cores are almost in contact. In the case of the two last-named species, the large size of the horn-cores accounts mainly for this. The general divergence of the horn-cores is similar in the Mongolian species and in *O. rothii* and *O. boulei*, but it is much greater in *O. wegneri*, *"Ovis" kuhlmanni*, *O.* (?) *mecquenemi* and apparently also in *O. atropatenes*. One of the most striking features of the Mongolian horn-cores is their uprightness. In most other species of *Oioceros* and in *"Ovis" kuhlmanni*, the horn-cores are tilted backward almost in the plane of the face. In *O.* (?) *grangeri* on the contrary the axis of the horn-cores forms an angle of no less than 55° with the facial axis and more than this in *O.* (?) *noverca*. In *O. rothii* and *O. atropatenes* they somewhat approach the condition found in the Mongolian species, the same angle being from 40° to 45°. This character seems to be a primitive one if we may judge by the uprightness of the horn-cores in the small antelopes of the Middle Miocene from Sansan. In both *O. wegneri* and *"Ovis" kuhlmanni* the horn-cores are situated quite behind the orbits. This position does not occur in the Mongolian species and apparently not in the other known species of *Oioceros*.

Although a long face seems, generally speaking, to be characteristic of the group, yet its length relative to that of the occiput is apparently greater in the Mongolian species than in most of the other species of *Oioceros*, with the exception of *O.* (?) *proaries* and *"Ovis" kuhlmanni*. In *O. wegneri* the face is also rather long. The defective character of most of the specimens prevents the ratio from being determined exactly, but *O.* (?) *mecquenemi* and *O. boulei* appear to have a much shorter face than any of the above-mentioned species.

Generally length of face is associated with long nasals and premaxillae, but the shortness of the occiput naturally affects the above ratio. In *O. boulei* the posterior end of the nasals lies just in front of the midpoint of the orbit, and their anterior end is far in front of P^2. In *O.* (?) *mecquenemi* and *O.* (?) *grangeri* the posterior end of the nasals is on a level with or in front of the anterior edge of the orbits. In *O.* (?) *grangeri* at any rate, the nasals terminate at least as far in front of P^2 as in *O. boulei*.

In *O. boulei* the nasals articulate with both lachrymals and maxillae, but whether the premaxillae run up into the opening which is left between the maxillae and the nasals as in *O.* (?) *grangeri*, *Capra* and to

some extent *Ovis*, or are very remote from the nasals as in *Capricornis* and *Nemorhaedus*, the imperfect preservation of the specimens does not permit us to say.

The angle between the cranial and facial axes varies considerably in the different species. It seems to be least in *O. boulei*, about 20°. In *O.* (?) *grangeri* it is about 30°; in *O. rothii* about 40°; in *O.* (?) *mecquenemi* about 45°; in *O.* (?) *proaries* about 50°; in *O. wegneri* and *"Ovis" kuhlmanni* about 90°.

Most of the species of *Oioceros*, in which the lachrymal fossa is preserved, have it deep. It is certainly so in *O. boulei*, *O.* (?) *mecquenemi* and *"Ovis" kuhlmanni*, and is probably but little deeper in the Mongolian species, though its anterior extension may be greater than in the first two species named. In *O. wegneri* the lachrymal fossa is said to be large but shallow.

The position of the fronto-parietal suture is different in *O.* (?) *grangeri* from what is the case in *O.* (?) *proaries* and probably *"Ovis" kuhlmanni*. In the Mongolian species it lies far forward as in *Nemorhaedus;* in the Samos species considerably to the rear, as in *Ovis*. It is impossible to infer what obtains in other species of *Oioceros* from the figures, descriptions or specimens which I have seen. The swelling round this suture is a feature of the Mongolian species which, so far as I am aware, does not exist in other species of *Oioceros*.

In the group we are considering, the occiput is known only in the species *O. wegneri*, *O.* (?) *proaries*, *"Ovis" kuhlmanni* and *O.* (?) *mecquenemi* in addition to *O.* (?) *grangeri* and *O.* (?) *noverca*. It is very decidedly longer in the two Mongolian species than in any of the others. The small area of the surface of the occipital is a marked feature of *O.* (?) *proaries* and *"Ovis" kuhlmanni*. In the other species named it is larger, in *O.* (?) *mecquenemi* largest of all. In none of the European and Maragha species do we find the extraordinary concavity of the occipital surface nor the extreme prominence of the lambdoid crest, which are so remarkable in the Mongolian species. As might be expected, in *O. wegneri*, *"Ovis" kuhlmanni* and *O.* (?) *proaries*, in which the bending down of the face on the occiput is considerable, the angle between the occipital and the parietal surface is very obtuse, but even in *O.* (?) *mecquenemi* the angle is much more obtuse than in *O.* (?) *grangeri*. In the Maragha species the foramen magnum and the condyles also appear to be larger.

I am not aware of the structure of the basicranium in any other species of *Oioceros* except *O.* (?) *grangeri* and *O.* (?) *mecquenemi*. In both of these the basioccipital is very similar, somewhat less triangular

in the Maragha than in the Mongolian species, but in any case very different from the quadrate shape of *Ovis* and *Capra*. In both species the posterior tuberosities are low and laterally expanded, but the median groove between them is deeper in *O.* (?) *mecquenemi* than in *O.* (?) *grangeri*. The anterior tuberosities are low but more expanded laterally in *O.* (?) *mecquenemi* than in *O.* (?) *grangeri*. The bullae are broken off in *O.* (?) *mecquenemi* but their outline seems to be similar to that in *O.* (?) *grangeri*, though they may have been somewhat longer. I do not think they can have extended far below the general surface of the basi-occipital.

The upper molars agree in all the species referred to *Oioceros* in respect to their quadrate outline and relative hypsodonty. Relative to the dimensions of the skull, the size of the molars is greater in the Mongolian than in other species of *Oioceros*. On the other hand, the premolar series is shorter. This is less noticeable in *O.* (?) *noverca*. In *O. wegneri* in particular, the premolar series is longer. P_4 is very similar in the species *O. boulei* and *O.* (?) *grangeri*, In neither case is the inner cusp united to the anterior and posterior wings, and the wings themselves are not at all complicated. In both there is a very deep furrow in the front third of the external wall of the tooth.

It remains now to compare the Mongolian skulls with those of various living forms, with the object of determining their most probable affinities.

The only genera besides the Oiocerines which regularly show a counter-clockwise torsion in the horn-cores are *Ovis*, *Pseudois*, and *Ammotragus*. In *Capra* the horn-cores are sometimes twisted, but generally in a clockwise direction. The expansion of the orbital roof is shown equally by *Ovis* and *Rupicapra*. It is less marked in *Capra* and still less so in *Myotragus balearicus* and *Nemorhaedus*, while in *Capricornis* the orbital rims do not project at all. At the same time the breadth at the frontals is extremely marked in *Capricornis*, though proportionately less so than in *Ovis*, *Rupicapra*, *Capra* and *Oioceros*.

The nasals in *Oioceros* (?) *grangeri* resemble *Ovis* rather than *Capricornis* and *Nemorhaedus* by their length, which is actually in excess of that usual in *Ovis*. On the other hand, their long articulation with the maxillae is like the condition in *Capra*, *Capricornis* and *Nemorhaedus*, but not like *Ovis*. The premaxillae, as in *Capra*, articulate both with the nasals and the maxillae. In *Ovis* there is a long articulation with the maxillae but none with the nasals, although the two bones are nearly in contact. In *Capricornis* and *Nemorhaedus* the premaxillae are very

remote from the nasals. The premaxillae exceed in length those of *Ovis*, *Capra*, *Capricornis* and *Nemorhaedus*, but in *Rupicapra* they are still longer. The fronto-nasal suture lies some way anterior to the orbits in *Ovis*, *Capra* and *Capricornis*. On the other hand, in *Oioceros* it is either on a level with or behind the anterior edge of the orbit. In *Rupicapra* its position is even more to the rear.

The position of the fronto-parietal suture in *O.* (?) *grangeri*, only 17 mm. behind the horn-cores, agrees nearly with that of *Capricornis* and *Nemorhaedus*. In *Capra* and *Ovis* it is much farther back, as is also the case in *Oioceros* (?) *proaries* and presumably in *"Ovis" kuhlmanni*. In consequence of the position of these two sutures, the frontals in *Ovis* are enormously long and the parietals short. Even in *Capricornis*, however, the frontals are longer than in *O.* (?) *grangeri* on account of the forward position of the fronto-nasal suture. *O.* (?) *grangeri* is midway between *Nemorhaedus* and *Ovis orientalis* in regard to the length of the frontals.

The course of the fronto-parietal suture, convex towards the rear, is different from that in any of the allied genera except *Rupicapra* and is in any case quite unlike that of *Ovis* in which the parietal indents the frontal at a right angle pointing towards the front.

The deep lachrymal fossa is paralleled in *Ovis*, but does not exist in *Pseudois*, *Ammotragus*, *Rupicapra* or *Capra*. A shallower one is found in *Capricornis*, while in *Nemorhaedus*, according to Pocock (1918, p. 135), although a fossa is not present, there is a small preorbital gland.

The basicranial region of *O.* (?) *grangeri* and *O.* (?) *mecquenemi* shows no resemblance to that of *Ovis* or *Capra*. In the living genera the basioccipital is broad and quadrate; the two anterior tuberosities are particularly strongly developed and laterally expanded, so that no interval is left between them and the bulla, and the basioccipital is actually wider in front than behind. In *Ovis* forward of this point, the basioccipital narrows abruptly, while at the same time the plane of its surface makes a definite angle with that of the basisphenoid. In *Capra* the basioccipital and the basisphenoid are in the same plane. In both genera the surface of the basioccipital is concave. In *Rupicapra* and *Oreamnus* the structure is very similar, though the anterior tuberosities are less prominent than in *Ovis*, so that the posterior portion of the basioccipital is the broader. On the contrary in *Oioceros* (?) *grangeri* the posterior tuberosities are strongly developed and a gradual narrowing occurs throughout the basioccipital and the basisphenoid, so that the shape is triangular. The anterior tuberosities are only slightly marked and the surface of the bone is convex. It is also much narrower and there

is a considerable interval between it and the bulla. The structure in most species of *Capricornis* and *Nemorhaedus* is almost identical with this, except that the basioccipital is rather broader especially in *Capricornis bubalina* which makes some approach to *Ovis*. In all these the bulla is small but most so in *Nemorhaedus*. In *Ovis* it is somewhat inflated. Its size and shape are very similar in *Oioceros*, *Capricornis* and *Pseudois*. *Oioceros* and *Pseudois* resemble one another most closely because of the size and shape of the vagina processus hyoidei, which is less wide than in *Ovis* and *Capricornis*. The small cleft in the inner wall of the bulla, which is visible in all the living genera mentioned but less so in *Ovis* and *Rupicapra*, is unnoticeable in *Oioceros* (?) *grangeri*. The position of the stylomastoid foramen and the foramen lacerum medium is more like the condition in *Capricornis* than in any of the other living genera. The foramen lacerum medium faces almost entirely downward instead of laterally.

The breadth of the occiput is relatively greater than in any of the living genera mentioned, but the difference is much less marked in the case of *Capricornis*.

Finally as to the dentition, the resemblance of *Oioceros* is to *Capricornis* and *Nemorhaedus* rather than to *Ovis* and *Capra*. The two former genera have square upper molars characterized by only a moderate degree of hypsodonty, in distinction from the narrow, strongly hypsodont upper molars of the two latter genera.

TAXONOMICAL CONCLUSIONS

It is evident that the nearest affinities to *Oioceros* (?) *grangeri* and the other Oiocerines are found in *Ovis* and its allies, *Capra*, *Rupicapra*, *Nemorhaedus* and *Capricornis*. Of these, *Ovis* and *Capra* are considerably more specialized than any of the others, on account of the extreme bending down of the face on the occiput, their large, twisted, complicated horns, the lateral expansion and hollowed surface of the basioccipital, the broad, high forehead, the large orbits, and the narrow, extremely hypsodont molars. So generalized are *Nemorhaedus* and *Capricornis* in most of these features that one could easily imagine some small, primitive, marginal species of one of these genera as the ancestor of both *Capra* and *Ovis*. At first sight it would seem that *Oioceros* (?) *grangeri* or *O. noverca*, which already possess the highly characteristic counter-clockwise torsion of the horns, might be the actual ancestor of *Ovis*, provided we can admit that the narrow, convex, triangular basioccipital of *Oioceros* (?) *grangeri* could, between the Sarmato-Pontian and the

Measurements of Species of Oiocerinae in Millimeters

	Oioceros (?) *grangeri*, sp. nov.			*Oioceros* (?) *noverca*, sp. nov.			*O. rothii* (Pikermi)	*O. rothii* (Maragha)	*O. atropatenes* (Maragha)	*O. boulei* (Maragha)	*O. wegneri* (Samos)	*O.* (?) *proaries* (Samos)	"*Ovis*" *kuhlmanni* (Samos)	*O.* (?) *mecquenemi*, sp. nov. (Maragha)
	A. M. 26508	A. M. 26509	A. M. 26510	A. M. 26223	A. M. 26501	A. M. 26507								
MEASUREMENTS OF SKULL														
Length from occipital condyles to front edge of premaxillae		277												
Length from occipital condyles to front tip of nasals	203											180		
Distance from occipital condyles to hinder edge of orbit	100				77?									?61
Distance from occipital crest to fronto-parietal suture	78											37?		?43
Distance from fronto-parietal suture to fronto-nasal suture	76									38		70?		?61
Distance from midpoint of orbit to occipital crest		102										?80		80
Length of nasals	app. 98									49				
Length of premaxilla		100												
Breadth of skull between external auditory meati	91				70						75	63?		66
Breadth of skull at orbits	125.5	123				100	app. 95	89		71	117?	86?	110?	?91
Breadth of skull behind orbits	62									?46	71	59	67	
Breadth of skull behind fronto-parietal suture	73	70								45		62		63

Breadth of palate between P^2	37									16	24	22	25	
Breadth of palate between M^3...	40	40								24	36	34	34	31
Height of occipital from occipital condyles to top of occipital crest.....	62				46.5									42
Height of face in front of P^2.....										27	42	36	37–40	
Height of face behind M^3.....	83									38	61	56?	67	?45
Distance between outer edges of occipital condyles.....	52.5				38						48			48
Distance between supraorbital pits.....	53			37.5				36		24				?30
Vertical diameter of orbit.....	38	39								27		42		
Horizontal diameter of orbit.....	41									29		43		
Length of horn-core from top of pedicle to tip.....	110						145	?145	106	?105	220?			
Longitudinal diameter of horn-core at base.....	39	32		26			31	29.5	20–21	20	52		53	?29
Transverse diameter of horn-core at base.....	35			26			26	22.5	17–18	20	51		38	?21
Distance apart of horn-cores at base of pedicles.....	28			18		23	17	19		19	25		18	?28
Distance apart of horn-cores at nearest approach.....	26			10		20?	16	19		18				
Distance apart of horn-cores at summit.....	92			34			117	?130						
Angle between cranial and facial axes.....	30°	25°					?40°	?42°		20°	90°	50°	90°	45°
Angle between direction of horn-core and plane of face.....	55°					65°	?44°		40°	16°	20°?		0°	15°
Length of upper molar series.....	58	55				39				27	39.5	42	39?	36
Length of upper premolar series..	33	33				24				18	27	28	26.5	
M^3 Antero-posterior diameter...	19		19							11	15	15	14?	12.5
M^3 Transverse diameter.....	18		18							9	13	15.5	13.5	12
M^3 Height of crown (almost unworn).....			19							11+		15		

MEASUREMENTS OF MANDIBLE

	Oioceros (?) *grangeri*, A. M. 26516	*Oioceros* (?) *noverca*, A. M. 26515
Length from angle to front edge of incisors	225 app.	
Length from posterior end of M_3 to front edge of incisors	162	
Length of diastema between P_2 and canine	60	
Length of lower molar series	57	44.5
Length of lower premolar series	29	22
Depth of ramus below M_3	35	
Thickness of ramus below M_3	17	12
Height of crown of M_3 (inside)	21+	19

Pleistocene, have assumed the broad, concave, quadrate shape, which characterizes the basioccipital of *Ovis*. However unlikely it might be thought that a change so important and one which affects such a particularly stable part of the anatomy should occur within that short period, one would not be prepared altogether to deny its possibility, were it not for another consideration which militates against the ancestry suggested. Both *Capra* and *Ovis* possess essentially the same type of basioccipital, but the horns of *Capra*, if untwisted, generally have a clockwise and those of *Ovis* a counter-clockwise torsion. Occasional exceptions, such as occur in *Capra pyrenaica* and *C. caucasica*, do not invalidate the following argument, since by a small heritable mutation an untwisted horn may develop torsion in either direction. One can scarcely imagine that this type of basioccipital arose independently on the two lineages of *Capra* and *Ovis*. Still less is it conceivable that the counter-clockwise-twisted horn of *Oioceros* (?) *grangeri* should have changed into the clockwise-twisted horn of *Capra*. It follows that the Ovicaprine type of basicranium must have been in existence contemporaneously or at any rate little later than the epoch at which *Oioceros* (?) *grangeri* lived and that the latter species represents a lineage which independently of *Ovis* developed a counter-clockwise torsion of the horns either at the same time or perhaps precociously. In the circumstances, unless we place *Ovis*, *Capra*, *Rupicapra*, *Nemorhaedus*, *Capricornis*, *Myotragus*, *Oioceros*, *Budorcas*, *Ovibos* (according to Pocock, 1918, p. 140) and their allies in one and the same subfamily, (a procedure which indeed I favor, though it is contrary to custom), we seem compelled to regard *Oioceros* (?)

grangeri and *O. noverca* as representatives of a distinct subfamily, *Oiocerinae*. *Rupicapra*, with its Ovine basicranium, upright, primitive horns, narrow muzzle and backwardly placed nasals, should equally be separated as a subfamliy distinct from *Nemorhaedus* and *Capricornis*. Pocock (1918, p. 140) has already advocated this for *Rupicapra* and makes yet another subfamily for *Budorcas*. As regards the other six species which have been referred to *Oioceros*, as well as *"Ovis" kuhlmanni*, the similarity of the basicranium of *O.* (?) *mecquenemi* to that of *O.* (?) *grangeri* affords good evidence of genetic affinity between these two, but until we become acquainted with the basicranium of the others, we are not in a position definitely to say whether all or any of them belong to the lineage of *Oioceros* (?) *grangeri* and *O. noverca* or to that of *Ovis*. Certain characters possessed by *Oioceros* (?) *proaries* and *"Ovis" kuhlmanni* seem more suggestive of an Ovine ancestry, in particular the backward position of the fronto-parietal suture, the large orbits, the large horns and the small occiput. On the other hand, the forward extension of the nasals and the quadrate upper molars point to an affinity with *Oioceros* (?) *grangeri*. I am, however, predisposed in favor of regarding them all as of the same lineage on account of the fact that so many species with counter-clockwise-twisted horns and having teeth and other characters at the *Nemorhaedus* stage of evolution lived at about the same geological epoch in Eurasia. Otherwise it is curious that we find no developmental stages between say *"Ovis" kuhlmanni* and true *Ovis* in the same Eurasiatic region, indeed that *Ovis* is entirely absent previous to the Pleistocene in spite of numerous finds of fossil antelopes in the Val d'Arno, Rousillon and Sénèze. The latter locality has even yielded a whole skeleton of *Nemorhaedus philisi* Schaub (1922, p. 558). If *Ovis* and *Capra* had sprung from some *Nemorhaedus*-like form either in another region or at a later epoch, this anomaly would disappear and we should merely regard the Oiocerines, including *"Ovis" kuhlmanni*, as a special group, which developed in many ways similarly to the sheep and goats but did not persist beyond the Pontian.

In conclusion I wish to express my thanks to Mr. E. H. Colbert and to Mrs. Margaret Colbert for the execution of the composite diagram of *Oioceros* (?) *grangeri* on page 8, and to the former for his kindness in measuring several specimens in the American Museum for me; also to Mr. and Mrs. John Germann for the drawings of teeth and the retouching of several of the photographs.

Comparative Ratios in Genera Allied to *Oioceros*

	Oioceros grangeri	*Oioceros boulei*	*Ovis orientalis*	*Capricornis sumatrensis*	*Nemorhaedus griseus*	*Rupicapra rupicapra*	*Capra walie*
Hinder edge of orbit to tip of premaxilla / Hinder edge of orbit to occipital condyles	$\frac{205}{97}=2.11$		$\frac{184}{87}=2.11$	$\frac{198}{108}=1.83$	$\frac{163}{88}=1.85$	$\frac{156}{59}=2.64$	$\frac{177}{97}=1.82$
Hinder edge of orbit to tip of premaxilla / Breadth of skull behind fronto-parietal suture	$\frac{205}{70}=2.93$		$\frac{184}{72}=2.55$	$\frac{198}{74}=2.67$	$\frac{163}{71}=2.30$	$\frac{156}{62}=2.39$	$\frac{177}{76}=2.33$
P^2 to tip of premaxilla / Breadth of skull behind fronto-parietal suture	$\frac{83}{70}=1.18$		$\frac{66}{72}=.91$	$\frac{89}{74}=1.20$	$\frac{59}{71}=.83$		$\frac{65}{76}=.85$
Length of nasals / Breadth of skull behind fronto-parietal suture	$\frac{98}{70}=1.40$	$\frac{49}{45}=1.09$	$\frac{96}{72}=1.33$	$\frac{93}{74}=1.26$	$\frac{82}{71}=1.16$	$\frac{74}{62}=1.20$	$\frac{90}{76}=1.20$
Length of premaxilla / Breadth of skull behind fronto-parietal suture	$\frac{100}{70}=1.43$		$\frac{94}{72}=1.30$	$\frac{83}{74}=1.12$	$\frac{74}{71}=1.04$	$\frac{156}{62}=2.39$	

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